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И.В. Татаренко

Открытый университет,
МК7 6АА, Милтон Кинес, Великобритания;
Московский педагогический государственный университет,
119991, г. Москва, Российская Федерация

Наблюдения за продленным покоем у редкого вида *Fritillaria meleagris* L.

Fritillaria meleagris – редкий вид, в основном, приуроченный к пойменным лугам и лесам. Для охраны вида необходимо учитывать его способность к продленному покою. Изучение продленного покоя *F. meleagris* было осуществлено в ходе 8-летнего мониторинга особей в популяции вида на охраняемом лугу Лаг Медоу в Великобритании. В популяции был наиболее распространен одно- и двулетний продленный покой. Максимальная продолжительность покоя составила 7 лет. 22% особей в популяции не переходили в состояние продленного покоя в течение периода наблюдений. Значительная вариабельность среди индивидуальных паттернов перехода в и из покоящегося состояния у разных особей в разные годы позволила предположить генетическую разнородность особей в качестве основного драйвера продленного покоя у данного вида. У покоящихся растений *F. meleagris* были описаны три морфологические состояния, включая ложный покой у особей, продолжавших рост под землей. Особенности продленного покоя у редких видов должны быть изучены в ходе мониторинга индивидуальных растений и использованы для моделирования популяционной динамики вида.

Ключевые слова: продленный покой, *Fritillaria meleagris*, популяционная динамика, охрана редких видов

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I. Tatarenko

Open University,
Milton Keynes, MK7 6AA, UK;

Moscow Pedagogical State University,
Moscow, 119991, Russian Federation

Having a break: Prolonged dormancy observed in a rare species, *Fritillaria meleagris*

Fritillaria meleagris L. is a rare species mainly associated with floodplain forests and meadows. Conservation of populations of this species needs to consider a key aspect of its life history – prolonged dormancy (PD). In *F. meleagris*, this was observed during 8-years monitoring of individual plants on the protected ancient Lugg Meadow in the UK. One-year PD was most frequently observed in the population, followed by 2-year PD. Seven-year dormancy was the longest recorded. Twenty two percent of plants didn't display PD during the observation period. Large variability in the patterns of individual plants submerging and re-emerging from dormancy in different years, suggested individual genetic heterogeneity as the main factor driving PD of the species. Three morphological states were identified in dormant plants of *F. meleagris* including a false dormancy in individuals which carried on growing below ground. Patterns of PD in rare species need to be studied on individually monitored plants and applied to models of population dynamics for species conservation purposes.

Key words: prolonged dormancy, *Fritillaria meleagris*, population dynamics, conservation

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Introduction

According to the dictionary, dormancy is the state in which a plant is alive but not actively growing. The concept of plant dormancy (seeds, buds, individuals) is built on the assumption that continuous growth for plants is the norm, and a break in growth is an enforced state evolved under harsh conditions associated with a season unfavourable for vegetation [Anderson et al., 2010]. If plants stayed below ground for longer than the season unfavourable for growth, sometimes up to several years, prolonged dormancy (PD) is the state achieved [Lesica, Steele, 1994]. By 2018, 108 species from 58 genera and 21 families were shown to have PD [Zhmylev et al., 2018]. This included observations on taxa in which plants were recorded as having no above ground organs during their vegetation season. The morphogenetic processes going in plants while they stay below ground, remain largely unknown, so plants were assessed as dormant until they sprout an aerial shoot. As a result, there has been little recognition of the terminological controversy concerning species with a life cycle and growth that largely occur below ground (e.g., mycotrophic orchids): they were classified as ‘dormant’ because of the absence of above ground organs [Shefferson et al., 2018].

Even though terminological uncertainties around PD have been acknowledged [Considine, Considine, 2016], they are not easy to solve [Zhmylev et al., 2018]. Despite increase in studies of PD in recent years [e.g., Shefferson, Kull, Tali, 2005; Ellis et al, 2012], the drivers of PD are still poorly understood [Shefferson et al., 2018]. The influence of environmental factors is apparent when an entire population of the species remains in PD for a year or more, e.g., desert plants sprouting out in wet years while staying dormant during the long-term droughts. The stress-factors like drought, flood, critically low or high temperatures have to reach a certain physiological threshold for the particular species in order to account for PD of the entire population. This scenario does not explain the situations when some individual plants, randomly distributed across the same habitat, remain below ground, while neighbouring plants continue to vegetate and flower. This could be due to the interspecific genotypic variability of dormancy [Gillespie, Volaire, 2017] or life history of the species [Shefferson et al., 2018].

PD was widely observed in orchids, probably because of the large number of long-term studies in their populations for conservation purposes [Shefferson et al., 2018; Zhmylev et al., 2018]. Indeed, conservation of rare species and their populations is hardly possible without understanding of PD, if the species has it in its life history. *Fritillaria meleagris* L. – Snake’s Head Fritillary is an iconic species of the British floodplain meadows [Jefferson,

Pinches, 2011]. It has become a rare and endangered species because of habitat loss due to change in agricultural practice not only in the United Kingdom, but across Europe [e.g., Corneanu, Popescu, 1981; Piórecki, 2001; Red Data..., 2008]. Population studies of the species are critically important for its successful conservation. Several populations were monitored in protected areas in Sweden [Zhang, 1983], Romania [Csergő, Frink, 2003], Russia [Zolotukhina, Zolotukhin, 2012], the UK [Rothero, 2018], and Hungary [Biró et al., 2019], however the role of PD in population dynamics was mentioned only by Zhang (1983). Even though PD in wild populations of fritillaries was acknowledged, dormancy patterns and extents were difficult to measure in short-term studies.

Eight-years monitoring of plants of *Fritillaria meleagris* on the protected ancient Lugg Meadow, Herefordshire, UK allowed individual plants to be followed with their annual appearance as flowering, vegetative, or non-emerging (dormant). Measurements of plant heights and number of leaves and presence of a flower were compared for the same individual before and after dormancy testing the hypothesis of physical plant size related to the possible dormancy [e.g., Jacquemyn et al., 2010]. Another aim of the monitoring project was to establish age-related morphological characters, e.g., if number of leaves reflects the plant age as it was suggested by Zhang (1983) and Vakhrameeva, Nikitina, Denisova (1983). Studying the plants excavated during their dormancy, was expected to clarify the morphological processes in plants remaining below ground.

To reveal the drivers of PD in *F. meleagris*, dormancy patterns were investigated, both in time-series and spatially. The hypothesis of individual genetic heterogeneity being a key driver of PD [Gillespie, Voltaire, 2017] was tested by observations of plant behaviour throughout 8 years of monitoring. As drainage of the site was found to have an effect on a spatial distribution of *F. meleagris* [Tatarenko et al., 2013], another hypothesis was tested if there any relationship between microtopography of the site and frequency of PD in the plants of *F. meleagris* located at different elevations across their habitat.

Materials and Methods

The site

Investigation of PD in *F. meleagris* was carried out on the nationally protected Lugg and Hampton Meadows Site of Special Scientific Interest in Herefordshire, UK, with consent of Natural England and Herefordshire Wildlife Trust as organisations responsible for the species conservation on the site.

This semi-natural meadow has been traditionally managed for hay in summer, followed by aftermath grazing in autumn-winter. The site floods every winter from the river Lugg, for 2–4 months. Alluvium soils are more than 120 cm deep, well-structured and well drained.

The fritillary population on Lugg Meadow is located in its northern part, occupying a relatively small area. It comprises about 1200–1400 plants, more than 97% of them were white-flowered. The overall population dynamic there was monitored on 110 1×1 m randomly located quadrats, revisited annually for 6 years of volunteer-based project “Flight of Fritillary” in 2012–2017 [Rothero, 2018]. The ratio of vegetative to flowering plants was found to be an informative characteristic of the population dynamics. Vegetative plants only slightly dominated over flowering plants in 2012, break even in 2013, following by 50% increase by 2016 (Fig. 1).

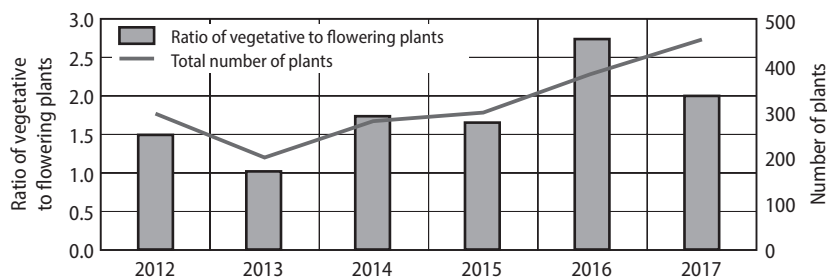


Fig. 1. Population dynamics of *Fritillaria meleagris* on Lugg Meadow, UK, in 2012–2017

Field observations

Plants for monitoring of PD were randomly chosen across the area of the meadow. One hundred twenty six locations of single plants and clones of *Fritillaria meleagris* were recorded in 2012 using high accuracy (up to 1 cm) differential GPS Leica RX1200. Careful observation was taken to ensure there were no other plants of the species in the area of 10×10 cm around the recorded plant. All locations were re-visited annually in 2013–2019. Surveys were conducted in middle to late April, approximately on the same dates every year. Two-week adjustments to the survey dates were made in 2016 and 2018 because of low spring temperatures and late flood, which delayed plant growth in those two years. Any new plants which were found in 10×10 cm area around each initially recorded individual, were also included into the survey in the year they were found, and monitored in subsequent

years. The following measurements of plants were made annually: height to the tip of the up-most leaf, number of leaves, flowering or vegetative status. In 2016–2019, the width of the leaf on plants having just a single leaf, was also measured.

In 2018, thirteen locations of non-emerged individual plants were excavated for the purpose of morphological assessment of dormant plants. The locations where plants were not seen above ground since 2012, were also excavated to check if plants remained dormant or had died. Three dormant bulbs were taken to the Lab for the detailed morphological investigation. Other bulbs were returned to their locations.

Results

In 2012, two hundred and three adult plants of *Fritillaria meleagris* were recorded in 126 location points on Lugg Meadow, in the area occupied by the population of the species. Among those (153 flowering and 50 vegetative) initially recorded at the fixed points, 91 were single-standing, and 112 were grouped in 43 clones of 2–7 ramets each. Over the course of monitoring period, 71 adult plants, which were dormant in 2012, emerged in 10×10 cm square around initially recorded points in later years. Vegetative plants had stems bearing 3–8 leaves, 8 plants re-emerged as flowering. Some adult plants had a large single “feeding” leaf (see more details below). Also, 268 juveniles were found in 10×10 cm squares in 2013–2019. They carried a single root leaf with 0,2–0,5 cm wide and 8–15 cm long leaf blade. Juvenile plants were considered to emerge from the germinated seeds. Adult vegetative and flowering plants, which appeared within 10×10 cm areas, were accounted as re-emerging from PD.

Based on knowledge about ability of the species to vegetative reproduction without noticeable spatial spread [Baranova, 1981; Tatarenko, unpubl.], very dense clumps of plants, all coming out of the ground within 2×2 cm area, were assumed to be the clones. Apart from 43 clones recorded in 2012, 13 more clones of 2–8 shoots each, re-emerged from PD within 10×10 cm areas in recorded locations during monitoring period. Both, disappearance of all shoots (ramets) of the clone into dormancy and their re-emergence were found to be highly synchronized (Table 1).

Number of years, when all ramets in the clone went dormant synchronically like clone 1 in Table 1, were compared to the number of years when some ramets behaved asynchronously like one in clone 3 in 2019 (Table 1). Data from 40 clones showed that number of years with synchronised appearance and disappearance of all ramets in the clone was 3 times higher than asynchronised cases (t-test, $p = 0.0001$).

Table 1

**Prolonged dormancy patterns in five clones
of *Fritillaria meleagris* on Lugg Meadow**

Clone number	2012	2013	2014	2015	2016	2017	2018	2019
1	d	d	d	f	f	f	v	d
1	d	d	d	v	v	f	v	d
1	d	d	d	v	v	v	v	d
1	d	d	d	v	v	v	v	d
2	d	f	f	f	v	d	d	d
2	d	f	f	f	v	d	d	d
2	d	f	f	f	v	d	d	d
2	d	f	f	f	v	d	d	d
2	d	v	f	d	d	d	d	d
2	d	v	f	d	d	d	d	d
2	d	v	f	v	d	d	d	d
2	d	v	f	v	d	d	d	d
3	f	d	d	v	f	f	f	f
3	f	d	d	v	v	f	f	f
3	f	d	d	v	v	f	f	f
3	f	d	d	v	v	f	f	d
3	f	d	d	v	v	f	v	v
4	d	d	d	v	d	v	d	d
4	d	d	d	v	d	v	d	d
4	f	d	d	v	d	f	f	d
5	d	d	d	d	d	d	d	v
5	d	d	d	d	d	d	d	v
5	d	d	d	d	d	d	d	v
5	d	d	d	d	d	d	d	v

Note: d – dormant, f – flowering, v – vegetative state of the individual plant in the certain year.

22% of plants recorded on Lugg Meadow in 2012 produced above ground shoots annually, for 8 years. Ten of them flowered every year; 20 plants had a break in flowering for 1–2 years but emerged as adult vegetative; and 5 other plants grew as adult vegetative for 4–7 years before setting flowers. 78% of plants recorded in 2012, had a break in vegetation above ground for different length of time. Eleven plants remained in adult vegetative state during all 8 years of observations, having 1–3 years episodes of dormancy, but never flowered. Based on overall number of 276 adult individuals recorded in 126 10×10 cm squares over 8 years, durations/frequencies of PD were distributed across individual plants as shown in Fig. 2. Two years was the most common overall duration of PD during this 8-year period, however, most of dormancy episodes were only 1-year long (Fig. 2). Three year episodes of PD were mainly recorded in plants which went dormant once, for 3 years (Fig. 2). Four-year episodes of PD, in contrast, were rare, recorded in just four flowering plants which re-emerged as flowering after 4 years below ground. In other plants, four-year overall dormancy came as a sum of the four 1-year dormancies or sequence of 1- and 2-year dormancies, arranged in different annual patterns. Most of 5-, 6- and all 7-year long episodes of PD were recorded in plants, which emerged from dormancy in 10×10 cm squares during the years of monitoring, not recorded in locations initially in 2012. All of them were adult vegetative plants, some of them bearing large “fee-ding” leaf.

Death rate in adult group was very low. Only one individual recorded in 2012 was confirmed to be dead by 2018. Among juveniles, 6% were recorded once in 2015, then stayed below ground for 4 years; there were no checks carried out to see if they were still alive in 2019 or not.

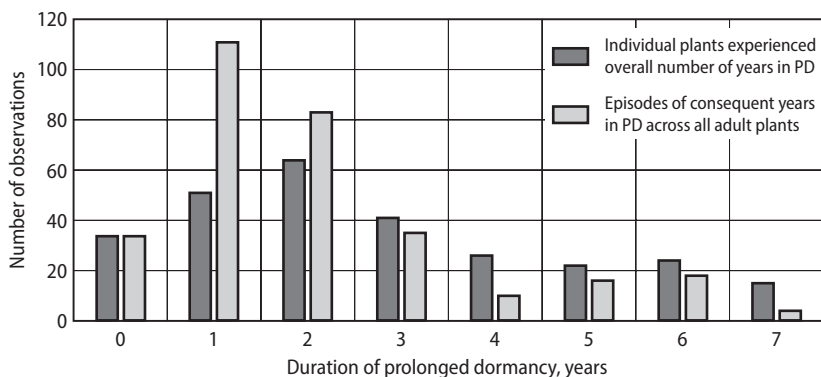


Fig. 2. Number of adult individual plants of *Fritillaria meleagris* experiencing PD of different combined lengths, and number of episodes of PD of different lengths

Overall, 167 different individual dormancy patterns (annual sequences of dormant and active status of individual plants) were observed among 231 adult vegetative and flowering plants with recorded episodes of PD. Even the first three years of observations showed 20 unique patterns (Fig. 3). Synchronised switches into/out of dormancy were mainly accounted to the plants in clones (Table 1).

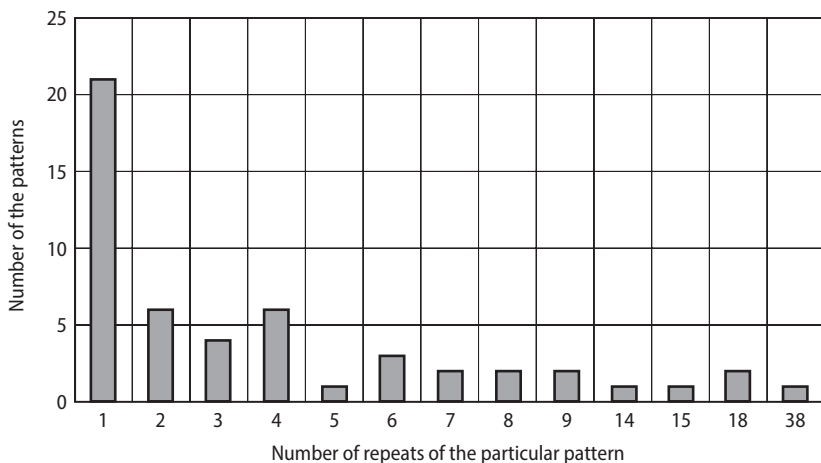


Fig. 3. Dormancy patterns in *Fritillaria meleagris* population on Lugg Meadow in 2012–2015

Some dormancy patterns of 268 juvenile plants appeared in 10×10 cm observation areas over 8 years, are shown on Table 2. During the period of monitoring, 12% of juvenile plants were followed to reach the flowering state. That took them from 2 to 6 years (average of 3 years); 33% of those plants experienced 1–4 years of PD between their first juvenile appearance and first set of flowers. More than 70% of all plants which appeared as juveniles in the observation areas in 2013–2019, experienced PD for 1–6 years (average of 2 years). 59% of juveniles went into PD after their first appearance; with other 12% vegetated for 2 years before PD. About 30% of juveniles had no PD recorded, however, a quarter of them were 1–2 years old individuals recorded at the end of observation period, in 2018–2019; those were likely to become dormant beyond the end of the data run.

Age groups (states) observed in fritillary population on the Lugg Meadow included (a) juvenile plants with 1 root leaf, 0.2–0.5 cm wide and 8–15 cm long, (b) adult vegetative plants with 3–7 leaves arranged along an aerial stem, and (c) flowering plants carrying flowers. Sequence of the age states

was one-directional from 1-leaved individuals to 3–7-leaved ones only in 6% of juvenile plants, which continued to increase their size and number of leaves from year to year. Nine percent of plants initially-recorded as juvenile, and 20% of plants initially-recorded as adult, had at least one reverse from having an aerial leafy stem back to the single leaf in subsequent year. In some plants, several reverses were recorded. Seven juvenile plants formed an increasingly large single leaf for 3–5 years before producing stem with a flower, missing out an “adult vegetative” state (aerial stem with 3–6 leaves). Such single root leaf was wider (0,8–2 cm) and longer (16–20 cm) than juvenile leaf. It was named a “feeding” leaf as the leaf size was similar to several narrow stem leaves put together. Occasionally, plants produced two root leaves, both developing from the bulb, not from the stalk. Bearing such “feeding” leaf was very common among the adult plants re-emerging from PD.

Table 2

**Some dormancy patterns in juvenile plants observed
over 8 years of monitoring**

Plant number	2012	2013	2014	2015	2016	2017	2018	2019
1	v	v	d	d	d	v	d	d
2	v	d	v	d	v	d	d	d
3	v	d	d	v	v	v	v	f
4	v	d	d	v	v	v	d	v
5	v	d	d	d	d	v	v	f
6	v	d	d	d	d	d	d	v

Note: d – dormant, f – flowering, v – vegetative state of the individual plant in the certain year.

There was a group of plants having intermediate size of the single leaves: 0,4–0,7 cm wide and 12–16 cm long, which could be equally large juvenile or weakened and small adult plants. Even with individually recorded plants, occasionally it was not feasible to distinguish between those two categories, so such plants were excluded from the analysis.

No significant difference in the heights of plants in 2012, was found between the group, which went dormant, and the group, which continue vegetation in subsequent year 2013 (t-test; $n = 86$, $n = 65$, respectively; $p = 0.18$). Most plants of *Fritillaria meleagris* re-emerged from PD in adult vegetative state (Fig. 4), having several leaves along the stem or one large “feeding” leaf.

Fewer occasions were recorded when plant re-emerged as flowering, especially after 3–5-year long episodes of PD (Fig. 4).

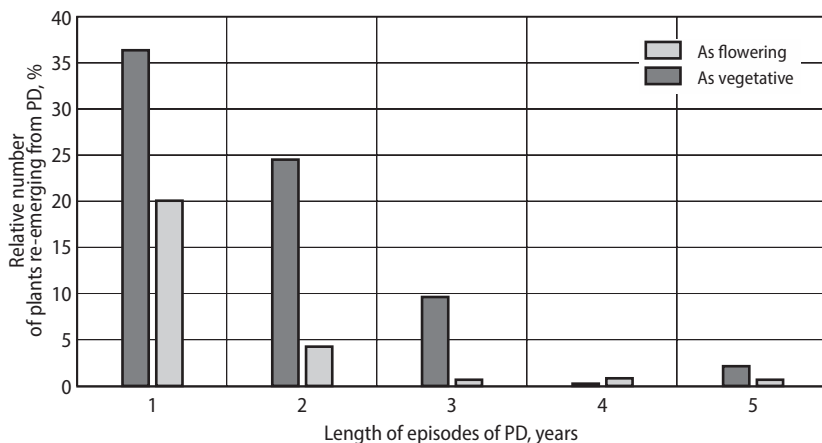


Fig. 4. Relative number of plants re-emerging from PD as adult vegetative or as flowering individuals depending on the length of the episode of prolonged dormancy

Numbers of leaves and heights of the plants entering dormancy were similar to the re-emerging plants, regardless the overall number of years they remained below ground (Fig. 5). Only the 2-year episode of PD had a significant effect on number of leaves before and after PD (Table 3). Variation in plant heights was very large (Table 3). Difference in plant heights in accordance with the length of episode of PD was significant only for 1-year PD (Table 3). Changes in the plant heights were synchronised by the year of observation (Fig. 6).

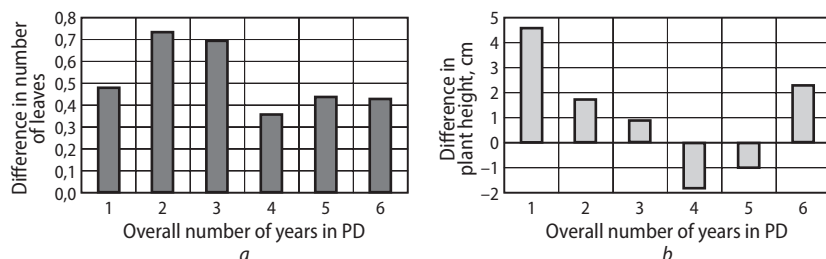


Fig. 5. Difference in number of leaves (a) and plant height (b) before and after PD depending on a number of years spent in PD

Table 3

**Difference in number of leaves and plant heights
before and after PD depending on a length of the episode of PD.
Statistical outputs of four t-tests**

Length of episode of PD	t-test	Number of leaves before PD	Number of leaves after PD	Plant height before PD	Plant height after PD
1-year PD	Mean	4.70	4.19	25.10	20.90
	Variance	1.12	2.40	70.00	61.40
	<i>n</i>	48	48	47	47
	<i>p</i> -value	0.08		0.02	
2-year PD	Mean	4.40	3.69	24.90	22.17
	Variance	1.43	2.65	74.80	80.90
	<i>n</i>	65	65	65	65
	<i>p</i> -value	0.01		0.09	
3-year PD	Mean	4.03	3.40	21.70	20.60
	Variance	1.56	3.25	71.00	47.00
	<i>n</i>	35	35	36	36
	<i>p</i> -value	0.09		0.52	
4-year PD	Mean	4.08	4.50	18.80	21.80
	Variance	0.80	3.00	51.20	67.96
	<i>n</i>	12	12	21	21
	<i>p</i> -value	0.47		0.18	

The frequency and duration of PD were analysed against topographical gradient on the site which ranged from 98.8 m above sea level at the lowest recorded point up to 99.25 m a.s.l. at the highest one. The area on Lugg Meadow, which was occupied by fritillaries, had variation in elevations within 40 cm. Majority of plants were found even in a smaller elevation range of 20 cm (Fig. 7). Plants with 1-year PD occurred at the same elevations as plants with no PD (t-test, $p = 0.8$). Very few plants with different durations of their PD occupied the lower elevations (Fig. 7).

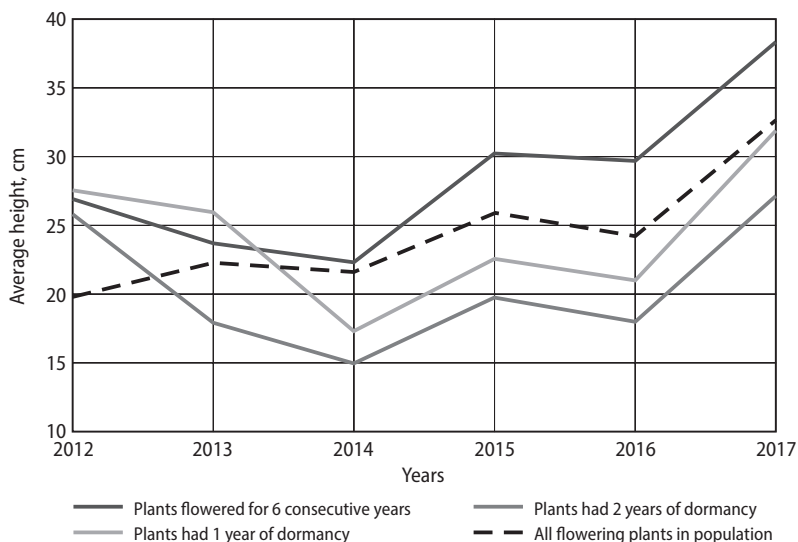


Fig. 6. Changes in the heights of flowering plants on Lugg Meadow in 2012–2017

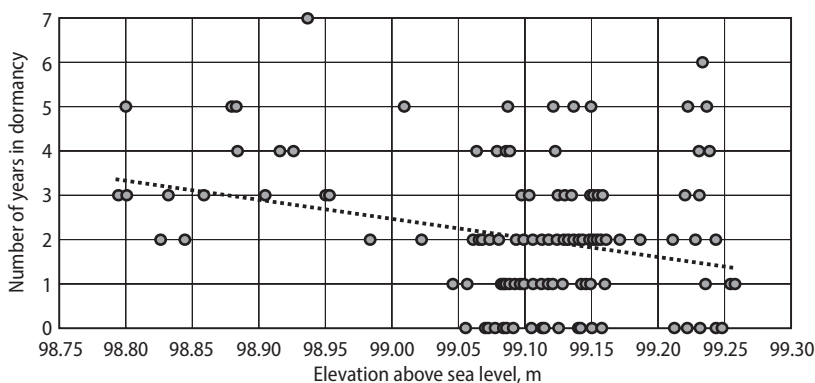


Fig. 7. Elevation range of locations of *Fritillaria meleagris* on Lugg Meadow in relation to the number of years, individual plants spent in prolonged dormancy

Excavation of dormant plants in 2018 revealed that their states below ground differed from each other. There were plants with two bulbs and dormant apical meristem (Fig. 8a, e). The plant shown on Fig. 8a had been dormant for 2 years, since flowering in 2015. It had an episode of growth below ground, forming a new bulb. Another dormant plant had only one bulb

(Fig. 8d). It was recorded as flowering in 2012, then remained dormant for 3 years, and re-emerged only in 2016 as adult vegetative for 1 year, before returning to PD for 2017 and 2018. It also had below ground growth, which resulted in vegetative reproduction and formation of the clone with the smaller plant with two bulbs (Fig. 8e), excavated next to the mother plant. Below ground growth is probably often accompanied by vegetative reproduction. Four juvenile-looking plants were found during excavation in location of the plant recorded once as flowering in 2012, and later remained dormant for 6 years (Fig. 9). Another example of vegetative reproduction of the plant recorded as flowering in 2012, is shown on Fig. 8c. Two plants were formed as a result of vegetative reproduction, one of them developed the adult vegetative aerial shoot in 2015, and then both of them carried on below ground growth, not forming the bulbs, but shoots bearing a sequence of succulent scales (Fig. 8c), internodes were up to 1 cm long, much longer than in normal shoots with bulbs (0.5–1 mm), so scales appeared to be spread along the stem. Plant shown in Fig. 8b, was flowering in 2017. In 2018 it started bud growth, but stopped it 5 cm below ground surface, all roots died, probably being affected by some external factors.

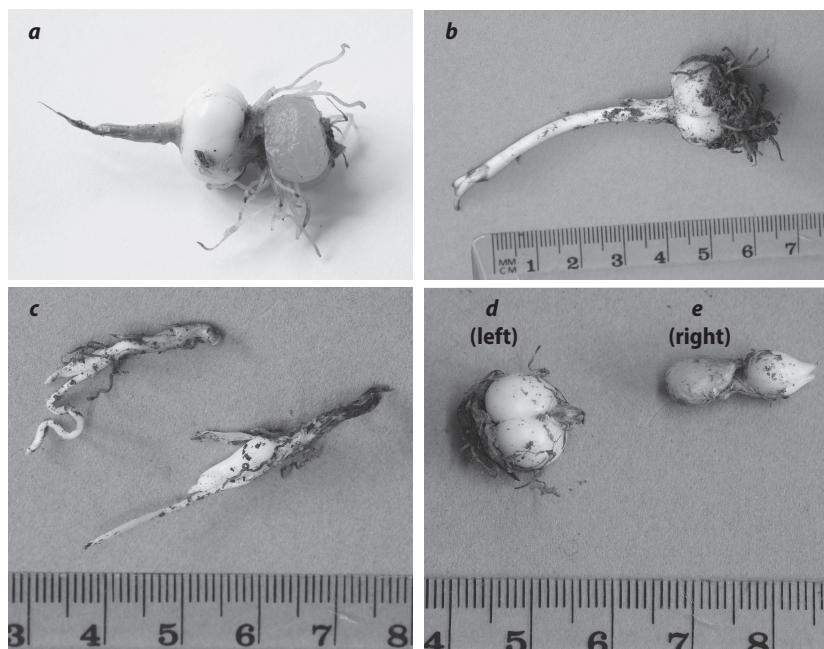


Fig. 8. Diversity of states of dormant plants of *Fritillaria meleagris* on Lugg Meadow in 2018

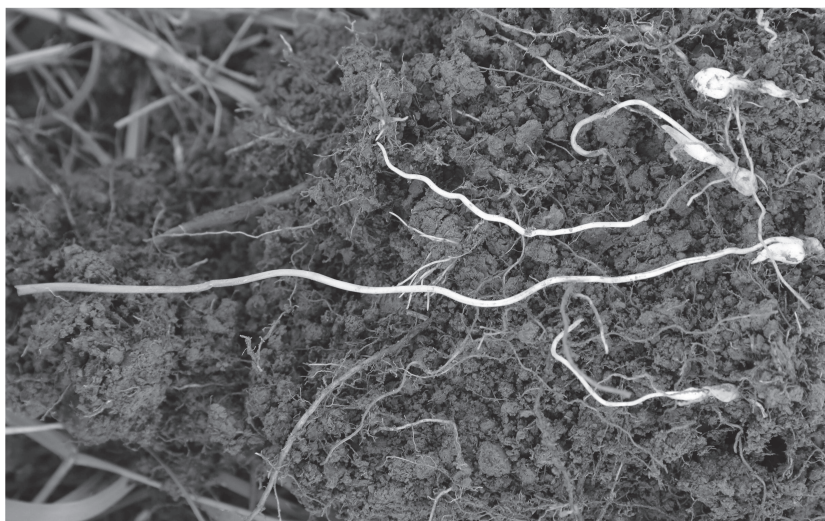


Fig. 9. Four plants formed below ground as a result of vegetative reproduction of one flowering plant (recorded in 2012) during its continuous 6-year dormancy

Discussion

Prolonged dormancy as an element of life-history, is not new for genus *Fritillaria*. It was previously recorded in *Fritillaria meleagroides*, a closely related species to *F. meleagris*, in experimental conditions where maximum length of PD was observed for 3 years [Markov, Idrisova, 1998]. In *F. meleagris*, PD was noticed in the wild population in Sweden [Zhang, 1983]. However, long-term specific monitoring of individual plants which aimed to identify the dormancy patterns in the species, has never been done before. Eight years of monitoring of individual plants of *F. meleagris* on Lugg Meadow in the UK confirmed that prolonged dormancy is an important feature of the species life-history.

As a property of the species life-history, PD in *F. meleagris* appeared to be similar to other Monocot species with annually replaced bulbs or root tubers as their main storage and perennating organs. Prolonged dormancy registered in Monocot bulbs, was shown to depend on plant size. In small-size plants like orchid *Ophrys sphegodes* Mill., *Cleistis bifaria* (*Cleistesiopsis bifaria* (Fernald) Pansarin & F. Barros), and species of genus *Caladenia*, 1-year dormancy was more common than any other length of time [Kéry, Gregg, Schaub, 2005; Tremblay et al., 2009; Hutchings, 2010]. In larger

plants like *Dactylorhiza* species [Vakhrameeva, 2000] and *Platanthera praeclara* Sheviak & Bowles [Sather, Anderson, 2010], 1 and 2 years dormancy periods were almost equally common. Rates of PD in *Allium ampletens* Torr. (Amaryllidaceae) studied in the permanent plots on Vancouver Island, showed the dormancy periods of 2 years were almost as frequent as 1-year periods, and 8% of plants were dormant for 3 years [Hawryski, Allen, Antos, 2009]. Similar rates of episodes of 1- and 2-year PD were recorded in this study of *Fritillaria meleagris* population on Lugg Meadow. Three-, four and five-year episodes of PD in *F. meleagris* were more common there than in the other species mentioned above. Substantial length of PD was rarely documented, firstly, because it required a very long-term monitoring, and secondly, because it is infrequent in populations [e.g., Hutchings, 2010]. Extent of PD up to 7 years was documented in few individuals of *F. meleagris* in this study, whereas 8-year dormancy was found in *Ophrys sphegodes* [Hutchings, 2010] and *Platanthera praeclara* [Sather, Anderson, 2010], and more than 10 years in *Neottianthe cucullata* [L.] Schlechter [Vakhrameeva, Zhirnova, 2003]. About 22% of monitored individuals of *Fritillaria meleagris* had no break in their appearance above the ground during 8 consecutive years. This is a relatively large proportion of population, however, in 25-years monitoring project on *Platanthera praeclara* [Sather, Anderson, 2010], the rate of plants survived with no dormancy was even higher: 43% in flowering and 30% in vegetative plants. Dormancy in juvenile plants was recorded as a regular event in *Fritillaria meleagris* population. The same trend was common in other bulbs, e.g., *Dactylorhiza* [Vakhrameeva, 2000], and *Allium ampletens* [Hawryski, Allen, Antos, 2009].

Suggestion of the interspecific genotypic variability of dormancy [Gillespie, Volaire, 2017] was supported by our study. 167 individual patterns of PD among adult plants and 14 patterns among juveniles were recorded during 8 years of observations in our project. This high annual variability among the plants going into/re-emerging from PD is difficult to explain by anything else but genetic heterogeneity of individual plants, which reacted differently to the same environment in the same habitat. Other possible explanations could be linked to a phenotypic plasticity of the species [Jäkäläniemi et al., 2011] or an epigenic regulation [Liu, Zhu, Abbott, 2015]. However, other evidence of genetic regulation of individual PD in *Fritillaria meleagris*, came from observation of clones. It was found that ramets in the clone experienced PD in a highly synchronized manner, disappearing into dormancy and re-emerging at the same years. Even some species with clonal growth were known to have PD [Kéry, Gregg, Schaub, 2005, Tatarenko, Kondo, 2006], dormancy patterns in clones were difficult to measure because of extensive

spatial spread of ramets. Having a very compact clonal growth in *Fritillaria meleagris* allowed recording of the synchronised dormancy patterns in clones for the first time.

Long-term study of individual plants over 8 years gave a good estimate of the species ontogenetic process. The life cycle of *F. meleagris* was described by Zhang (1983), who suggested a consequent changes in number of leaves from one in juveniles up to 3 in semi-adults, and 4–6 in adult individuals. This sequence of continuous increase in the number of leaves from year to year was observed in 6% of plants in our study. Multiple reverses of plants having several leaves on the aerial stem back to having a single root leaf, were recorded as a common pattern of fritillary's ontogenesis, including re-emergence from PD. The size of single “feeding” leaf was equal to the sum of 3–5 normal narrow leaves on the stem of adult vegetative or flowering plant. That implies that photosynthesis can go with the similar rate while an energy expense on formation of the above ground stem can be avoided. Adult vegetative plants of another *Fritillaria* species, *F. koidzumiana* Ohwi have single root leaf; aerial stem bearing several leaves develops only in flowering individuals [Kawano, Masuda, Hayashi, 2008]. Reverses from multiple leaves to the single leaf, as well as from the bigger leaf to the smaller leaf, in the life cycle, were also recorded in *F. koidzumiana* [Kawano, Masuda, Hayashi, 2008]. That can be a way of balancing an individual energy budget after experience of environmental stress.

Individual plants remaining in adult vegetative state for many years without setting flowers, is not a well-known phenomenon. The common assumption is that plants go through all subsequent stages of their life-cycle [Zhang, 1983; Vakhrameeva, Nikitina, Denisova, 1983]. Eleven adult plants of *F. meleagris* were found as non-flowering during 8 years of observations, having dormancy episodes for 1–3 years. The longer observation period could probably extend this value, as, for example, in *Platanthera praeclara* maximum survivorship for non-flowering plants was 17 years with dormancy [Sather, Anderson, 2010].

A hypothesis about weaken and small plants going into dormancy [e.g., Jacquemyn, Brys, Jongejans, 2010; Jäkäläniemi et al., 2011] was not confirmed with *Fritillaria meleagris*. All individually monitored flowering plants had similar heights at the beginning of observations in 2012, before half of them went dormant in 2013, while another half carried on a regular seasonal growth. There was a tendency for smaller sizes of plants re-emerging from PD.

Which external factors could drive PD in *F. meleagris*? The majority of research in plant dormancy has been done in dry habitats, suggesting PD is a survival mechanism in the habitats with dramatic fluctuation in water

resources [Boeken, 1991; Vaughton, Ramsey, 2001; Hawryzki, Allen, Antos, 2009; Gremer, Crone, Lesica, 2012; Gremer, Sala, 2013]. Floodplain habitats with *Fritillaria meleagris* experience an excess of water during flood events in winter, shortage of water occurs occasionally in summer time. However, dry period on British floodplains is unlikely to affect fritillaries, which have their seasonal break in vegetation in the summer. Moreover, the plants showed clear preference for locations on the floodplain with continuous and consistent drainage of the soil during summer months [Tatarenko et al., 2013].

Mainly as an adaptation to harsh seasonal extremes of Mediterranean climate, the alternation of root summer dormancy and winter growth appeared to be a critical survival strategy for some monocotyledons [Shane et al., 2009]. Dormancy probability in some orchids and lilies, was shown to correlate with spring temperature [Shefferson et al., 2001; Miller, Antos, Allen, 2004; Kéry, Gregg, Schaub, 2005], which probably affects root growth. Several studies showed effect of root growth on shoot apex development [e.g., Hao et al., 2014]. The regulation mechanism was associated with root length. The effect of the root length on shoot apex development was observed in *Tulipa systola* [Boeken, 1991] – it was the root system which stopped growing because of temperature and moisture regime, and then the bud followed.

Little was known about root emergence and growth in fritillaries *in the wild*. As we observed in the pot cultivation, roots start growing in late autumn, and persist through the winter months being no longer than 5–7 cm. In the very early spring or even late winter, root growth is resumed, and up to 40 roots are formed during March; their length reaches 20–40 cm [Tatarenko, unpublished]. Different conditions of root systems observed in the dormant plants of *Fritillaria meleagris* could explain a lack of shoot development in those individuals. In the plant shown on Fig. 8b, the roots were damaged and mainly dead, which could cause a break in the bud growth and no formation of the aerial shoot. The dormant Fritillary plant shown on Fig. 8a had living roots, their number and length were not sufficiently big, and the bud development was not even initiated. Two plants shown on Fig. 8d had no roots at all. The plants found growing below ground (Fig. 8c and Fig. 9) had 2–3 living and relatively long roots each, which probably helped initiation of leaf growth, however, the leaf blades were never formed, and plants remained below ground. Such “false” dormancy has been known in cultivation of lilies, when “dormant” lily bulblets continue to generate new scales at the same rate as before [Delvallée, Paffen, De Klerk, 1990]. In lily, the induction of dormancy does not correspond to a decrease of metabolism but to a switch in the development of the primordium: the primordium can no longer develop into a leaf, but only into a scale [De Klerk, 2012]. The question where

do the dormant plant obtain energy for growth, was answered by Gremer, Sala, Crone (2010), who showed dormant plants gaining as much nonstructural carbohydrates as photosynthetically active plants, an increase most likely due to remobilization of structural carbon, whereas carbon starvation, on the other hand, could be responsible for the bud dormancy [Tarancón et al., 2017].

Dormancy is important for a perennial growth of plants [Rohde, Bhalerao, 2007], where it plays two opposite roles in senescence processes [Tuomi et al., 2013]. Older *Astragalus scaphoides* (M.E. Jones) Rydb. plants had declining annual survival probabilities and reproductive value, suggesting senescence. *Silene spaldingii* S. Watson showed the opposite pattern for reproductive value that increased with age, indicating negative senescence [Tuomi et al., 2013]. Based on very limited observations of excavated dormant plants on Lugg Meadow, it is difficult to suggest, if vegetative reproduction in the dormant plants was a sign of senescence, similar to the senescent partitioning of other perennial species [e.g., Zhukova, 2012]. On the other hand, it can be seen as a process of re-juvenation [e.g., Tatarenko, 1996], when new plants developed from an adult individual have juvenile appearance and sizes and begin new life cycle.

Considering fritillaries local preference to the areas which drains well through the summer [Tatarenko et al., 2013], a correlation between PD frequency and micro topography was expected to be significant. Plants in the ditches may delay their growth until water is resided, and flower a month later than main part of the population situated on the higher ground [S. Holland, personal communication]. In such situations, the plants can be easily overlooked and not recorded in the main count. That could potentially lead to the situation when dormant plants were considerably overestimated [Hill, Garton, 2017]. However, in our study the number of plants growing at the lower elevations was small (Fig. 7). Under recording them in some years wouldn't make much difference to the results.

Conclusion

This monitoring project allowed to establish patterns of prolonged dormancy in *Fritillaria meleagris*, which must be considered in population studies of the species for conservation purposes.

One- and two-year episodes of PD were most common in Fritillary population, both among adult and juvenile plants. Seven-year extent of PD was recorded. Most flowering plants re-emerged from PD as adult vegetative.

Individual genetic heterogeneity was suggested to be a main driver of PD in an absence of extreme climatic events. Synchronous disappearance and re-emergence of the clones supported the hypothesis of genetic drivers of PD.

For population studies, the age groups suggested by Zhang (1983) were generally correct apart from interpretation of 1-leaved plants. Not only juvenile plants have 1 leaf. Adult plants can have a large single root leaf instead of forming aerial stem bearing several leaves. Also, adult plants of *Fritillaria meleagris* can re-emerge from prolonged dormancy having a large root leaf. Some plants vegetated for 8 years, never going into the flowering state of the life cycle.

There was no confirmation found that smaller plants of *F. meleagris* were entering PD more often than the bigger ones. However, the sizes of the plants re-emerging from dormancy, were significantly smaller in episodes of 1- and 2-year PD.

Excavated dormant plants were found in three different morphological states: 1) true dormancy of apical meristem; 2) “physiological” dormancy – when plants started growing but stopped, being affected by some external factors; 3) false dormancy – when bulbs kept growing below ground.

Population dynamic models must include three possible morphological states of the dormant plants, as well as population heterogeneity in PD.

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Сведения об авторе / About the author

Татаренко Ирина Васильевна – доктор биологических наук; научный сотрудник Школы исследований окружающей среды, Земли и экосистем, Открытый университет, Милтон Кинес, Великобритания; старший научный сотрудник Учебно-научного биологического центра, Московский педагогический государственный университет

Irina V. Tatarenko – PhD, Dr. of Sci.; Research Associate at the School of Environment, Earth and Ecosystem Science, Open University, Milton Keynes, UK; Research Fellow at the Center of Teaching and Research in Biology, Moscow Pedagogical State University

ORCID: <https://orcid.org/0000-0001-6835-2465>

E-mail: tulotis@yandex.ru